Importance of age structure in models of the response of upper trophic levels to fishing and climate change

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There is a growing effort to use predictions of the physical state of the ocean under climate change to forecast the response of marine ecosystems. Many of these forecasts use ecosystem models rather than age-structured population models to describe upper trophic level (UTL) species. We illustrate the potential effects of climate on age-structured populations, then illustrate the ways in which ecosystem models might not depict adequately: (i) long-term changes in abundance, and (ii) variability attributable to cohort resonance. We simulated two generic species with different life histories, a short-lived semelparous species (e.g. salmon), and a long-lived iteroparous species (e.g. cod). For both species, juvenile survival was varied, first with white noise, then with the Pacific Decadal Oscillation as environmental signals. Variability in recruitment increased with fishing and became particularly sensitive to forcing at time-scales near the mean age of reproduction, consistent with the cohort resonance effect. Ecosystem models without age structure do not predict this behaviour, particularly when the ecosystem model incorrectly predicts the effective steepness of the stock–recruitment relationship, or the age structure is approximated by a stage-structured model. We suggest that ecosystem models of UTLs include full representations of age structure, fitted to available population data.

Keywords: age structure, climate, fisheries, population modelling, upper trophic levels.

Introduction

As evidence solidifies that human activities are altering global climate (IPCC, 2007), there has been increasing development of models that attempt to project the effects of climate change on marine resources. Many of these models are based on statistical or dynamical downscaling of results from global climate models (GCMs; Spak et al., 2007; Tabor and Williams, 2010) to produce regional-scale physical scenarios that then drive coupled physical–biological models. A primary interest in the development of these models is the effects of varying climate on the fish and invertebrates targeted by global fisheries (Brown et al., 2009; Lindegren et al., 2010), reflecting the general concern regarding the combined effects of fishing and climate (Perry et al., 2010). As such, these models typically include a representation of one or more upper trophic levels (UTLs). The dynamics of the UTLs in the model are driven by some combination of physical variability from the downscaled GCM and an intervening model, such as a nutrient–phytoplankton–zooplankton model (Megrey et al., 2007), or a more comprehensive ecosystem simulator. The model of the UTL could be an age- and size-structured model similar to those currently used in stock assessments (van Kirk et al., 2010), but because of computational constraints, models to assess impacts of global change often use a simpler, approximate formulation to mimic the age structure

present in real UTL populations (reviewed in Plagányi, 2007, and Travers et al., 2007). Because of the great importance of these projections of future food resources, there is a need to ensure that such models represent faithfully the likely response of UTL populations to climate change.

Recent advances in our understanding of the behaviour of age-structured populations indicate that the representation of age structure could be of particular importance in predicting the response of populations to climate change. There is growing awareness that age-structured populations can essentially filter out certain frequencies in a random environmental signal (Greenman and Benton, 2005) and amplify those frequencies by exciting modes of variability in the population dynamics that would be locally stable in the absence of random variability (Greenman and Benton, 2003). For example, stochasticity in annual recruitment can produce a phenomenon termed cohort resonance, which results in cycles with period equal to the mean age of spawning (Bjørnstad et al., 2004), and fishing can intensify this effect (Worden et al., 2010). The importance of this phenomenon to predicting the influence of climate change on UTL dynamics stems from the fact that both climate change and increased fishing could shift the mean age of spawning, and the frequency of environmental forcing signals could change with climate. A change in the mode of variability or the forcing

spectrum could either increase or decrease the excitation of that mode, resulting in more or less variable fishery stocks. Greater variability generally diminishes sustainability, necessitating a management response.

The physical drivers of environmental forcing of marine populations tend to have specific spectral properties that vary on decadal scales and that could be altered by climate change. For example, the El Niño–Southern Oscillation phenomenon typically varies on time-scales of 3–5 years, with occasional periods of slower variability. However, its frequency spectrum has been observed to vary in the past (Cobb et al., 2003) and has been projected to change in future (Timmermann et al., 1999).

A variety of ecosystem models has been used to assess the response of marine ecosystems to climate change, and they approximate age structure in many different ways. Because they are complex models, focused on entire ecosystems, they sacrifice some detail in their representation of age-structured populations (Aydin, 2004). It is important to understand what is being sacrificed in this effort to achieve greater holism (Hollowed et al., 2000). With the focus on trophic relationships, rather than on population dynamic relationships, critical parameter values, such as those determining the stock–recruitment curve, might not be represented accurately (Plagányi and Butterworth, 2004). A second departure from true age structure is the adoption of a simplified approximation to an age-structured model. In particular, multiple age classes are often lumped into stages or discrete size classes, based on trophic considerations, or to increase computational efficiency (Walters et al., 2000; Christensen and Walters, 2004; reviews by Plagányi, 2007; Fulton, 2010). The direct consequence of such approaches is that age-specific information is lost as individuals transition between stages or discrete size classes, which affects the predicted responses of populations to the environment.

Here, we describe recent results in the theory of age-structured populations and demonstrate how the spectral sensitivity of age-structured populations undergoing various intensities of fishing might respond to existing or altered environmental forcing signals. We illustrate these phenomena using two examples, a generic long-lived iteroparous species representative of an Atlantic cod (genus Gadus) and a generic short-lived semelparous species representative of a Pacific salmon (genus Oncorhynchus). We then compare the generic cod response to the responses that would be projected: (i) with various errors in population parameters that are likely to arise in ecosystem models (Plagányi and Butterworth, 2004), and (ii) using a computationally simpler age-structured model and a stage-structured model. These comparisons demonstrate how models that do not resolve age structure in UTL species might produce substantial inaccuracies in forecasts of population abundance and variability in a changing climate.

## Developments in age-structured population dynamics

Research into the theory of population dynamics has recently identified characteristic modes of behaviour beyond those seen in earlier analyses focused on equilibrium conditions and deterministic population stability. These additional behaviours involve stochastic excitation of natural modes that would be stable without stochastic forcing. The behaviour of age-structured models with density-dependent recruitment can be described for linearized models that describe the response of a population at equilibrium to a small perturbation (as in Worden et al., 2010). The behaviour of such models is described by the sum of a number of characteristic modes representing different ways that a stable population returns to equilibrium after perturbation: either via geometric decay or in dampened cycles with a particular frequency. If a population is subject to constant stochastic perturbations from equilibrium, the characteristic modes tend to be repeatedly excited and they can become a dominant feature of population behaviour. The combination of the different modes causes the populations to be more sensitive to some frequencies than others. Populations can, therefore, filter out selectively certain frequencies in the environmental signals and amplify them. We refer to this characteristic of population behaviour as the spectral response of a population or its spectral sensitivity to different environmental time-scales.

Recently, populations dynamics researchers have identified the importance of cycles with period equal to the dominant age of reproduction (T), a mode that is deterministically stable, but can be excited by stochasticity. Heightened sensitivity to frequencies near $1/T$ in the environment, an effect termed cohort resonance, was identified in the context of fish populations by Bjørnstad et al. (1999, 2004). A key feature of cohort resonance regarding climate change is that increased sensitivity to frequencies near $1/T$ in the environment is accompanied by increased sensitivity to very low frequencies (Bjørnstad et al., 1999, 2004). This aspect makes it difficult to determine whether observed trends in abundance arise from (i) gradual change in the environment slowly altering a demographic parameter (e.g. survival), or (ii) trends in abundance that arise from heightened sensitivity of the age-structured population to random low-frequency variability in the environment.

The recent finding that fishing generally increases the effects of cohort resonance enhances its importance to climate change (Worden et al., 2010). Cohort resonance is intensified by a reduction in the adult survival rate, such as that which could result from an increase in the fishing rate or a decline in adult survival because of climate change. This finding indicates our ability to distinguish low-frequency variability associated with cohort resonance from deterministic changes in survival will be confounded. A second recent result is that variability in individual growth rate can have a greater effect on the cohort resonance mode than variability in survival (Worden et al., 2010). The ability to observe the cohort resonance mode depends on the variable being observed, because catch and abundance time-series will be skewed more towards lower frequencies than recruitment series (Botsford, 1986; Worden et al., 2010).

There are several examples of population behaviour with the apparent characteristics of cohort resonance. Populations of sockeye salmon (Oncorhynchus nerka) from Bristol Bay in Alaska and the Fraser River in British Columbia exhibit cycles with period equal to the dominant age of reproduction (Figure 1). The consistency of cohort resonance varies among sockeye stocks from constant cycles (Figure 1a and f) to intermittent cyclic behaviour (Figure 1b, g, d, and i) to a lack of consistent cyclic behaviour (Figure 1, h, e, and i). The period of cycles differs between the Fraser River, where the dominant age of spawning is 4 years, and Bristol Bay, where the dominant age of spawning is 5 years. The nature of these cycles has received much attention for decades, and Myers et al. (1998) identified what is essentially the cohort resonance mechanism as a potential cause of the well-studied cycles in sockeye salmon in the Fraser River. Cohort resonance could also occur in some iteroparous stocks. Bjørnstad et al. (2004) identified a peak with period 2–3
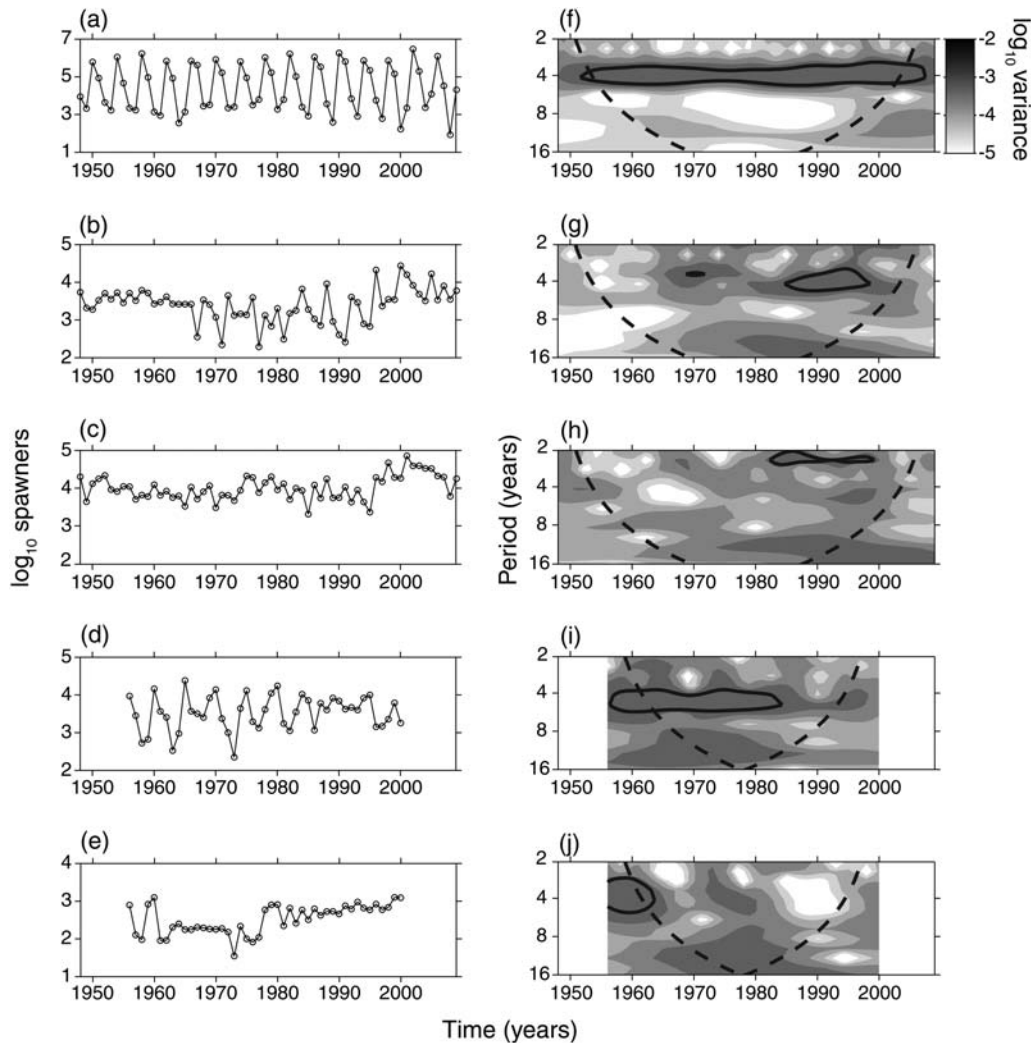
Figure 1. Representative (a – e) time-series and (f – j) wavelet spectra of sockeye salmon (*O. nerka*) stocks in the Fraser River (British Columbia, Canada) and Bristol Bay (AK, USA) regions. Shading in (f – j) indicates local variance at each period, relative to the variance of the original time-series, and the dashed line indicates the cone of influence, outside which edge effects distort the spectrum. The thick contour encloses regions with variance significantly greater ($\alpha = 0.95$) than a red-noise process with the same lag-1 autocorrelation as the original time-series. Significance should be discounted outside the cone of influence. Power spectra were calculated using Morlet mother wavelet (Torrence and Compo, 1998). Stocks are (a, f) Lake Shuswap (Fraser River), (b, g) Raft (Fraser River), (c, h) Pitt (Fraser River), (d, i) Kvichak (Bristol Bay), (e, j) Alagnak (Bristol Bay). Data courtesy of M. LaPointe (Fraser River) and R. Peterman (Bristol Bay).

years in the spectrum of a time-series of Atlantic cod counts from Skagerrak, Norway. That period corresponds to the dominant ages of spawning for this stock, which lives only 6 years (their Figure 1). Their model of the cohort resonance mechanism using parameter values from this population displayed a peak at periods just >2 years (their Figure 3).

Models and methods

To represent the behaviour of typical age-structured populations, we used generic representations of two taxa, salmon and cod, which span a range of life histories from a short-lived semelparous species to a long-lived iteroparous species. We used generic models rather than those of a particular species, primarily to underscore the general nature of the results. The behaviour we are demonstrating is not a prediction of specific population state (e.g. catch, age structure, abundance) at a certain time in future, but rather a mode of population behaviour reflected in the spectral sensitivity

of the population (i.e. the relative sensitivity to environmental variability on different time-scales). As such, the comparisons we make here do not depend on the specific population structure and parameter values for a particular salmon or cod stock, but only on a reasonable representation typical of these two taxa of UTL fish populations with annual age structure.

The point of departure for all models used here is a linear age-structured matrix model with a non-linear egg–recruit relationship, resulting in a model with a finite equilibrium. For the generic iteroparous species (cod), the model has the form

$$
\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} R[P(t)] \\ s_1(t)x_1(t) \\ s_2 x_2(t) \\ \vdots \\ s_{n-1}x_{n-1}(t) \end{pmatrix}, \tag{1}
$$

where $x_i(t)$ is the number of individuals in age class i at time t, $P(t) = \sum_{i=1}^{n} p_i f_i x_i(t)$ the egg production resulting from the age-specific probability of spawning, p_i, and the age-specific fecundity rates, f_i, $R(P) = aP/(1 + \beta P)$ the Beverton–Holt egg–recruit relationship, and s_i gives the age-specific survival rate from age i to $i + 1$. Hereafter, we refer to the number of fish entering the first age class, $R[P(t)]$, as "recruits".

The semelparous (generic salmon) model takes the form

$$
\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} R[P(t)] \\ (1-p_1)s_1(t)x_1(t) \\ (1-p_2)s_2 x_2(t) \\ \vdots \\ (1-p_{n-1})s_{n-1}x_{n-1}(t) \end{pmatrix}, \quad (2)
$$

where the multiplicative $(1-p_i)$ terms account for the fact that spawning is an additional source of mortality in a semelparous species.

In both models, environmentally driven survival in early life is in the first survival term, s_1. Survival is a function of instantaneous natural mortality, M_R (age 1) or M (constant across older age classes), and age-specific fishing mortality, F_i', and is given by

$$
s_i = \exp(-M - F_i'), \text{ for } i > 1, \text{ and} \quad (3.1)
$$
$$
s_1(t) = \exp\lfloor -M_R - F_1' + \xi(t) \rfloor, \quad (3.2)
$$

where $\xi(t)$ is a time-dependent forcing signal. Stochasticity, therefore, enters via variation in the rate of survival from age 1 to age 2. Values for all parameters of the iteroparous and semelparous models are given in Table 1. In simulations, the values of survival, s_1, that were >1.0 were set to 1.0.

In both the iteroparous and semelparous models, spawning, fecundity, and survival rates depend on size-at-age, which is modelled with a von Bertalanffy growth model:

$$
L_i = L_\infty \{1 - \exp[k(t_0 - i)]\}, \quad (4)
$$

with parameters, k, the growth rate, L_∞, the asymptotic average length, t_0, the time when an individual would be of length zero, and the length–weight relationship

$$
w_i = \theta L_i^{\phi}, \quad (5)
$$

with allometric scaling parameters θ and ϕ. Spawning probability is an increasing function of length and follows a cumulative normal distribution with mean length at first spawning μ_p and spread about the mean size given by σ_p:

$$
p_i = \frac{1}{\sigma_p \sqrt{2\pi}} \int_{-\infty}^{L_i} \exp\left(-\frac{(l - \mu_p)^2}{2\sigma_p^2}\right) dl. \quad (6)
$$

The parameters μ_p and σ_p were chosen such that ~ 10 and 90% of individuals mature at ages 3 and 4, respectively, and essentially 100% are mature at ages ≥ 5. Age-specific fecundity was taken to be a linear function of weight,

$$
f_i = m w_i + f_0. \quad (7)
$$

In the iteroparous case, we assumed that fecundity is simply proportional to weight ($f_0 = 0$), whereas in the semelparous case, fecundity is assumed to be essentially constant across spawning ages ($m = 0$; Groot and Margolis, 1991).

Fishing mortality increases with size following the function $F_i' = \rho_F(L_i)F$, where F represents the constant fishing effort, and the vulnerability to fishing at age i is given by a cumulative normal distribution:

$$
\rho_F(L_i) = \frac{1}{\sigma_F \sqrt{2\pi}} \int_{-\infty}^{L_i} \exp\left(-\frac{(l - \mu_F)^2}{2\sigma_F^2}\right) dl. \quad (8)
$$

For the iteroparous species, we assumed that recruitment to the spawning stock and to the fishery are simultaneous, so that $\mu_F = \mu_p$ and $\sigma_F = \sigma_p$. For the semelparous species, we assumed

Table 1. Parameter values used in the models.

Parameter	Description	Value	
		Iteroparous	Semelparous
α	Slope at origin of Beverton–Holt (fish eggs^{-1})	9.64×10^{-7}	9.64×10^{-7}
β	Beverton–Holt saturation parameter (fish^{-1})	9.64×10^{-11}	9.64×10^{-11}
n	Maximum age (years)	20	5
a	Age of maturity and initiation of fishing	4	4
L_∞	Asymptotic mean length (cm)	100	100
k	Growth rate (year^{-1})	0.3	0.3
t_0	Time such that $L = 0$ (years)	-0.1	-0.1
θ	Allometric length–weight scale	8.0×10^{-6}	8.0×10^{-6}
ϕ	Allometric length–weight exponent	3.0	3.0
μ_p	Mean length at first maturity (cm)	65.66	65.66
σ_p	Standard deviation of length at first maturity (cm)	3.990	3.990
m	Slope of weight–fecundity relationship (eggs kg^{-1})	5×10^5	0
f_0	y-intercept of weight–fecundity relationship	0	1.401×10^7
M_R	Instantaneous natural mortality of recruits (year^{-1})	0.6	0.6
M	Instantaneous natural mortality (year^{-1})	0.2	0.2
F	Baseline fishing mortality (year^{-1})	$0-0.694$	$0-2.083$
μ_F	Mean length at onset of fishing (cm)	65.66	53.64
σ_F	Standard deviation of length at onset of fishing (cm)	3.990	5.385
σ	Standard deviation of forcing signal	0.3275	0.3275
f	Adult fecundity, lumped model (eggs kg^{-1})	2.561×10^6	–

that fishing mortality precedes spawning, because the majority of fishing mortality is sustained before the spawning migration is complete in most Pacific salmon fisheries.

For both taxa, the amount of reproduction at each age determines the population equilibria and dynamic behaviour (Figure 2a and b). The generic cod is a reasonably long-lived species with a substantial number of individuals reaching 20 years of age in the unfished state, whereas the generic salmon has a maximum age of 5 years (i.e. all 5-year-olds spawn). The generic cod have a modal age of spawning that declines from 6 to 4 years with fishing, whereas for the generic salmon most individuals spawn at age 4 years, with some spawning at ages 3 and 5 years. For age-structured models with density-dependent recruitment, the equilibrium level of recruitment can be represented graphically on a stock–recruit plot of the number of recruits vs. total annual egg production. It is the point where a straight line through the origin with slope 1/(lifetime egg production) intersects the egg–recruit curve (Sissenwine and Shepherd, 1987). Lifetime egg production (LEP) is often normalized by dividing by its value with no fishing (Goodyear, 1993), which is referred to as the fraction of LEP (FLEP). In the fisheries literature, LEP and FLEP often appear as eggs per recruit and spawning potential ratio, respectively. The Beverton–Holt curve was parametrized such that the population persists if FLEP > 0.2 [i.e. the slope at the origin of the curve is $(0.2 \times \text{unfished LEP})^{-1}$]. Given their differences in longevity, the dependence of FLEP on fishing

mortality rate F differs between species (Figure 2c). Because the dynamic behaviour of each species depends on its equilibrium relative to the point of collapse, we illustrated the dependence of dynamic behaviour on fishing level for the same equilibrium recruitment and egg production (i.e. same values of FLEP). This was done by choosing the fishing mortality rates for each species that will produce the desired value of FLEP (Sissenwine and Shepherd, 1987; Figure 2c).

We demonstrated the behaviour of these generic species using two environmental forcing scenarios: (i) the response of the populations to white noise (i.e. equal variance at all frequencies) in the environment for several different levels of adult survival, and (ii) the response of the populations to an existing climatological time-series from the 20th century as an example. The former reveals the general changes in spectral sensitivity of the populations to environmental variability at all frequencies. The latter illustrates how the changing spectrum of an environmental variable and the various levels of spectral sensitivity of an age-structured population combine to produce the variability expected from such UTL age-structured populations. We chose the Pacific Decadal Oscillation (PDO; Mantua *et al.*, 1997) to demonstrate this, because it is widely known that it has been associated with variability in the productivity of north Pacific ecosystems (Peterson and Schwing, 2003) and its temporal variability is mostly at the decadal scale (approximately tens of years), with occasional outbreaks of variability on time-scales as low as 4 years.
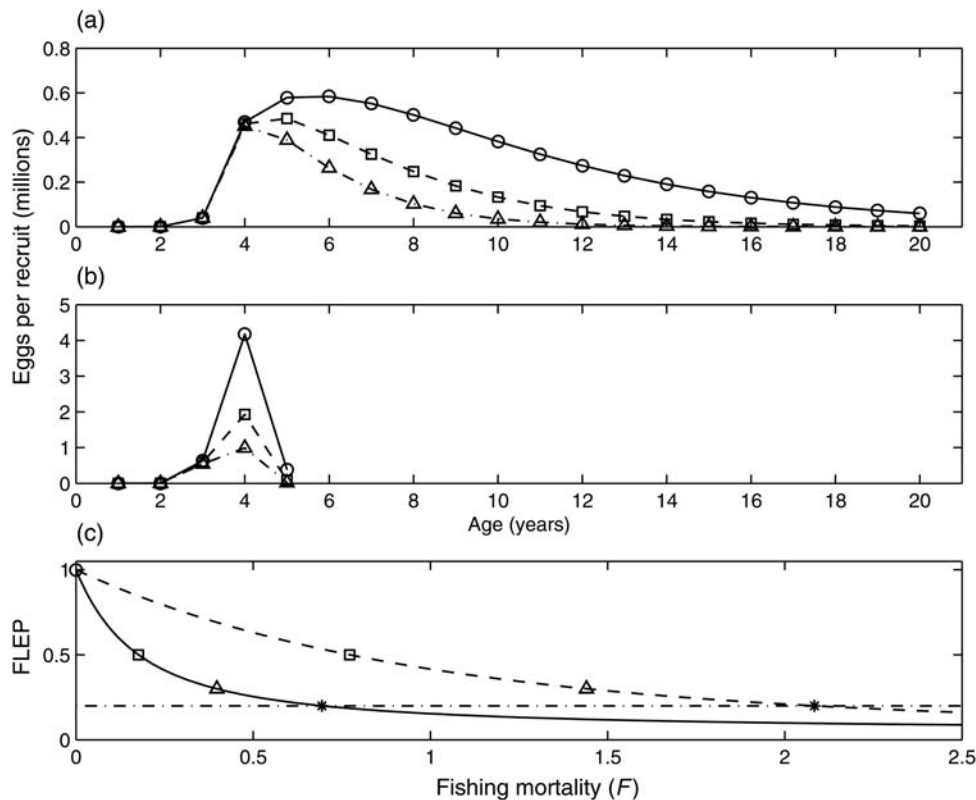
Figure 2. The distribution of reproduction over age for the generic iteroparous species (e.g. cod; a) and the generic semelparous species (e.g. Pacific salmon; b). Each point is the product of the survival from age zero to that age times the fecundity at that age. For each species, the distribution is given for three different levels of fishing corresponding to three different levels of the FLEP. The dependence of FLEP on the fishing mortality rate F for the generic iteroparous (cod) species (solid line) and semelparous (salmon) species (dashed line; c). In all three plots, circles indicate no fishing (FLEP = 1.0), squares indicate moderate fishing (FLEP = 0.5), and triangles indicate heavy fishing (FLEP = 0.3). The dash–dot line in (c) indicates FLEP = 0.2, the level below which the population would collapse because of overfishing, and asterisks are plotted at the collapse point for each model.

The white noise scenario was implemented by letting parameter $\xi(t)$ in Equation (3.2) be a random variable drawn from a normal distribution with mean 0 and s.d. 0.3275. For the PDO scenario, we calculated annual average values of the PDO time-series for years 1900–2009, normalized the series to have zero mean and s.d. 0.3275, then set $\xi(t)$ equal to the negative of the normalized PDO value in year t. In this way, the variability in juvenile survival had a coefficient of variability of ~0.34.

To illustrate how ecosystem models that might appear to contain a reasonable approximation to an age-structured fish population could fall short of representing the expected behaviour of an age-structured population, we evaluated (i) the consequences of errors in population parameter values that can occur in ecosystem models (cf. Plagányi and Butterworth, 2004), and (ii) the use of computationally simpler approximations to models with annual age structure. For the former, we chose two sources of error that might affect population behaviour: (i) the slope of the egg–recruit relationship at the origin (α), and (ii) the age of maturity and initiation of fishing (a). We illustrate the potential consequences of these errors by applying them to the otherwise correct representation of the age-structured population, the generic iteroparous population.

To explore the effects of using a simpler approximation of an age-structured population, we first used a "lumped" population model, where fully age-structured information is retained for juvenile age classes, but adults are lumped into a single multiage stage. This is a commonly used approximation (Botsford, 1992; Hastings and Botsford, 1999) that is also the representation of age structure frequently adopted in ecosystem models (Ecopath with Ecosim: Walters *et al.*, 2000; Christensen and Walters, 2004; multispecies age-structured assessment model: van Kirk *et al.*, 2010). We chose an age-structured model with three juvenile ages followed by a lumped adult stage. We therefore assumed that maturation and vulnerability to fishing mortality occurred at a single, fixed age, rather than changing more gradually. For a stock that matures at age 4, this resulted in the model

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ x_4(t+1) \end{pmatrix} = \begin{pmatrix} R[fx_4(t)] \\ s_R(t)x_1(t) \\ s_J x_2(t) \\ s_J x_3(t) + s_A x_4(t) \end{pmatrix}, \quad (9)$$

with $s_R(t) = \exp[-M_R + \xi(t)]$, $s_J = \exp(-M)$, and $s_A = \exp(-M - F)$. The single *per capita* fecundity parameter, f, was chosen such that the unfished equilibrium recruitment of the lumped model and the fully age-structured iteroparous model would be equal. $R[f\, x_4(t)]$ is the same Beverton–Holt stock–recruitment function as in the generic iteroparous model.

For the second approximation, we evaluated the effects of converting an age-structured model to a model using stages composed of multiple age classes. This included models formulated in terms of stage- and size-structured models whose numerical solutions move specific fractions of abundance between size classes (Hall *et al.*, 2006). For the purposes of illustration, we converted the 20-age generic iteroparous model to a model with ten stages. This approximation is similar to that taken in early versions of the Atlantis model, where for vertebrate groups with lifespans >10 years, the age structure was represented for ten stages, with each stage representing one-tenth of the lifetime (Fulton *et al.*, 2004; Brand *et al.*, 2007).

Regarding the parameters from the age-structured iteroparous model, the stage-structured model is

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_{10}(t+1) \end{pmatrix} = \begin{pmatrix} R[P(t)] + \dfrac{s_1(t)}{2}x_1(t) \\ \dfrac{s_2}{2}x_1(t) + \dfrac{s_3}{2}x_2(t) \\ \dfrac{s_4}{2}x_2(t) + \dfrac{s_5}{2}x_3(t) \\ \vdots \\ \dfrac{s_{18}}{2}x_9(t) + \dfrac{s_{19}}{2}x_{10}(t) \end{pmatrix}. \quad (10)$$

Note that for each stage, the first term represents the entry of new individuals into that stage and the second term represents individuals remaining in the stage. Fecundity within a stage is simply taken to be the arithmetic mean of the corresponding fecundities-at-age from the age-structured model, so that now the egg production function is

$$P(t) = \frac{p_3 f_3 + p_4 f_4}{2}x_2(t) + \cdots + \frac{p_{19}f_{19} + p_{20}f_{20}}{2}x_{10}(t).$$

The factors of one-half in all survival terms result from the average stage duration of 2 years (if the stage duration is τ, the fraction remaining in the stage is $1-1/\tau$, whereas the fraction leaving is $1/\tau$; for $\tau = 2$, both values are equal to $1/2$). Note that accounting for age structure is lost using this approach; a fraction $1/2$ passes from stage i to $i+1$ in each time-step, but there is not a fixed duration for stage i.

We compared all these approximations with the generic cod model for the case of a population with annual variability in age-1 survival where fishing increased from $F = 0$ (FLEP = 1) at year zero to the value of F corresponding to FLEP = 0.2 (the collapse point) at year 100. This allows a composite view of the effects of environmental variability and decreasing survival.

In the analyses of the responses to the white noise environmental signal and the PDO, as well as in our analyses of the
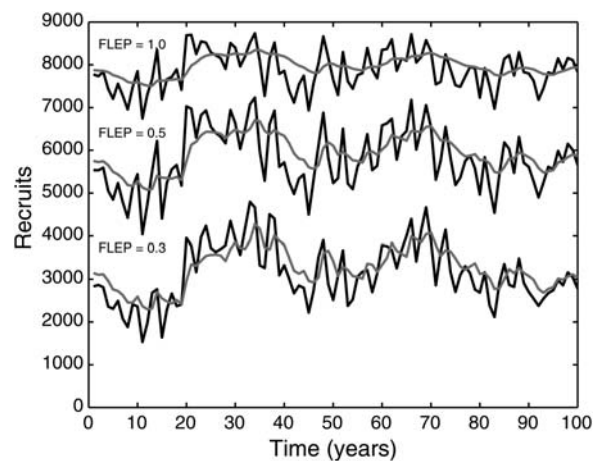
Figure 3. Recruitment time-series for the generic cod species (grey lines) and the generic salmon species (black lines) from simulations with fluctuations in the survival rate driven by white noise with a constant mean and a *CV* of 0.338. The three series for each generic species are unfished (top plot), fished to FLEP = 0.5 (middle plot), and fished to FLEP = 0.3 (bottom plot).

approximations to true age structure, we used spectral analysis to investigate further the time-scales of variability. Specifically, we used wavelet spectra (Torrence and Compo, 1998) to reveal variability at specific frequencies localized within the time-series. This approach allowed us to detect resonance at particular modes within a stochastic time-series. Spectra were calculated using the Morlet mother wavelet (Torrence and Compo, 1998).

Results

The fully age-structured models of both generic species displayed cohort resonance in the time-series resulting from white noise with a constant mean, both at a period near 4–6 years and at a multidecadal time-scale (30–40 years; Figure 3). The low period variability was much more obvious in semelparous species and appeared in the iteroparous species only at the heavily fished level (FLEP = 0.3). Variability increased with fishing (Figure 3, Table 2), with the cohort resonance becoming stronger. The means of recruitment for each species declined with fishing and they were virtually the same at each value of FLEP, as expected from their identical equilibrium conditions. The coefficient of variation (CV) and the s.d. of recruitment of both species increased with fishing, except that the s.d. of the two fished cases of the semelparous species were approximately equal (Table 2).

The spectral response of the two species can be viewed in two different ways: (i) as the long-term, general sensitivity of the population to variability at different time-scales (Figure 4), and (ii) as the variation in the spectra over time in response to a specific random time-series of white noise (as in Figure 3; Figure 5). The former indicates that as fishing increases, the responses of the two species are similar in two respects: (i) that the total variance in each (i.e. the integral over each line in Figure 4) increases,

and (ii) that the cohort resonance, i.e. relative sensitivity to time-scales near the modal age of reproduction and to long periods, increases (Worden *et al.*, 2010). The two species differ in that the generic salmon has greater cohort resonance than the generic cod, where short-period (5 years) resonance appears only at FLEP = 0.3.

The temporal variations in spectral responses (Figure 5) from the time-series in Figure 3 demonstrate how single realizations reflect the general behaviour in Figure 4. As an indicator of the effects of fishing on the spawning age distribution (Figure 2), the mean age of spawning is plotted on Figure 5. The iteroparous species displayed greater variance at longer periods than shorter periods, consistent with Figure 4. For the iteroparous unfished and the moderately fished cases (FLEP = 0.5), there were bouts of variability with a period of 8–16 years, with actual cohort resonance, i.e. variance at a period of 4–6 years, appearing only in the heavily fished case (FLEP = 0.3) near the mean age of spawning, which was 6 years for that level of fishing. This is consistent with the spectra in Figure 4 and the dominant age of reproduction in Figure 2. The semelparous species displayed the cohort resonance effect of occasional bouts of variability at a period near its mean age of reproduction (4 years) with no fishing, and slightly stronger bouts when fished. For both generic species, variability at long time-scales increased with fishing.

Our ultimate interest is in how age-structured UTLs will respond to actual changes in the spectra of forcing signals in the environment. The spectrum of the PDO used here as an example has predominantly decadal scale variability, but with occasional bouts of variability in the range of time-scales of 3–8 years, for example, from the early 1930s to the late 1960s (Figure 6). The spectral response of the generic species in

Table 2. Changes in mean and level of variability for populations forced with environmental variability with a coefficient of variability of 0.3275.

	White noise						PDO					
	Iteroparous (cod)			Semelparous (salmon)			Iteroparous (cod)			Semelparous (salmon)		
FLEP	Mean	s.d.	CV	Mean	s.d.	CV	Mean	s.d.	CV	Mean	s.d.	CV
1.0	7 965	214.6	0.0269	7 878	451.2	0.0573	8 031	288.6	0.0359	7 940	519.5	0.0654
0.5	5 924	405.9	0.0685	5 806	702.5	0.121	6 054	557.2	0.0920	5 927	820.8	0.1385
0.3	3 240	461.8	0.143	3 127	700.0	0.224	3 449	714.0	0.207	3 322	936.2	0.282
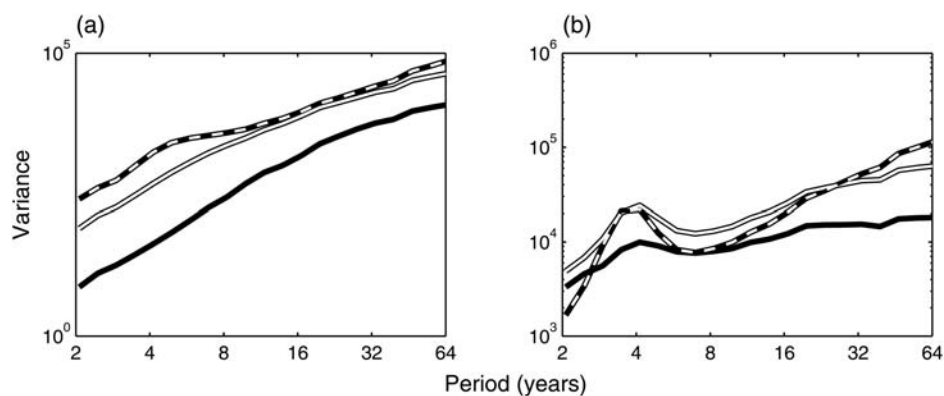
Figure 4. Time-averaged variance spectra from a wavelet analysis of recruitment time-series like those in Figure 3, but of length 16 384 years, of (a) generic cod and (b) generic salmon. Levels of FLEP are 1.0 (solid black), 0.5 (white with black edges), and 0.3 (black and white dashes).
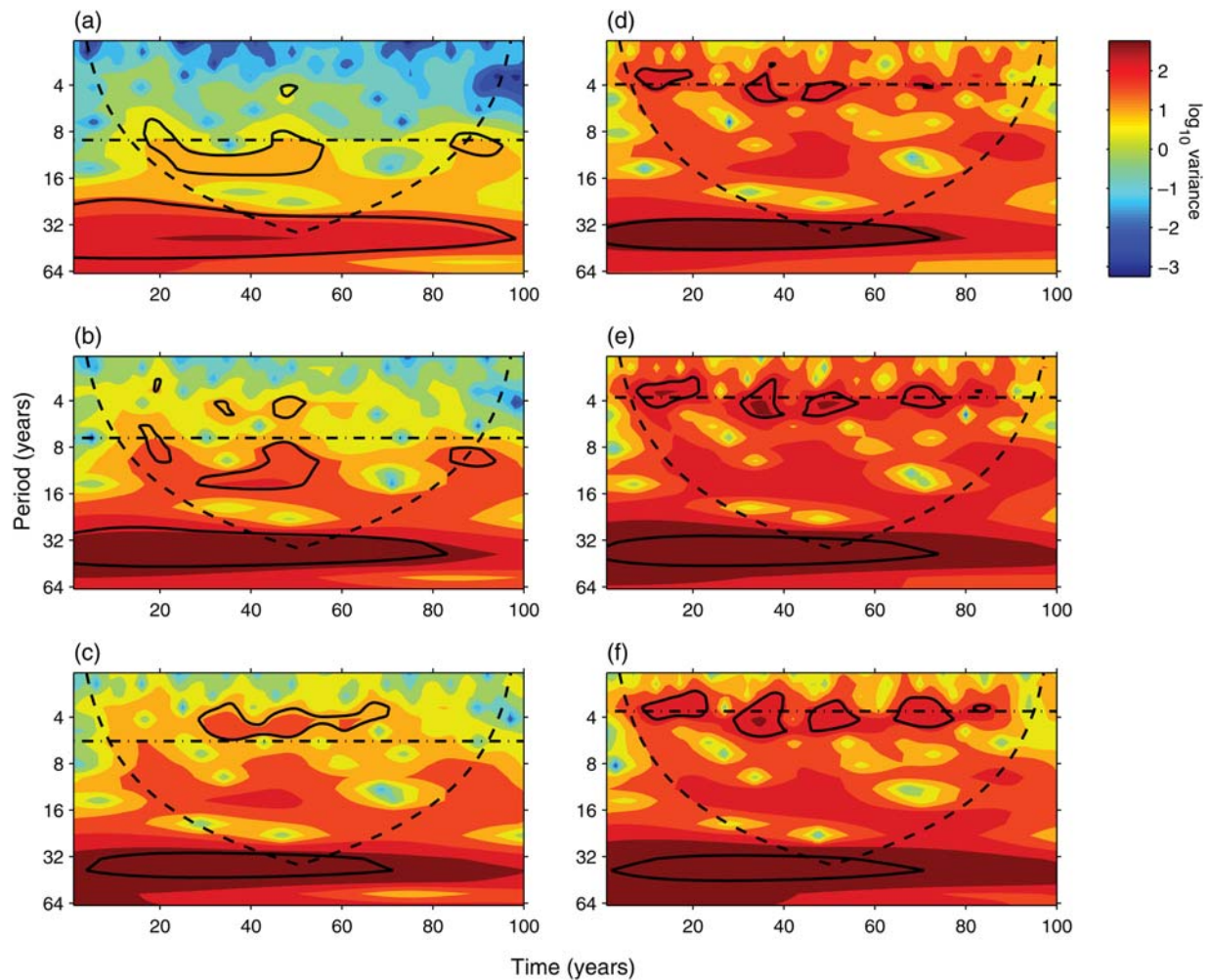
Figure 5. Wavelet spectra for the recruitment of the generic cod species (a–c) and generic salmon (d–f) time-series in Figure 3. The three levels of fishing are unfished (a and d), fished to FLEP = 0.5 (b and e), and fished to FLEP = 0.3 (c and f). The horizontal dash–dot line in each panel is the mean age of reproduction (*T*) for each case. Other lines and units as in Figure 1.

Figures 4 and 5 to white (uncorrelated) forcing essentially displays the relative sensitivity to variability at different frequencies. The spectrum of population variability that would result from a population driven by the PDO should essentially be the product of the population sensitivity to variability at each frequency (Figure 4) times the spectrum of the PDO at that frequency (Figure 6). Hence, we would expect recruitment to be more variable at times and frequencies where the spectra in Figures 4 and 6 have coincident high values. Based on the PDO spectrum (Figure 6) and the spectral sensitivity indicated in Figure 4, we would expect to see the bout of climatic variability at periods 3–8 years between the early 1930s and the late 1960s to be stronger in the salmon population than the cod population, and to be skewed by population filtering towards the frequencies to which the populations are most sensitive, i.e. periods near 4–5 years for salmon and slightly greater frequencies for cod (Figure 4).

The time-series of recruitment resulting from survival forcing with the inverse of the PDO (Figure 7, Table 2) indicated a general increase in the relative amount of variability with increased fishing as in the white noise forcing, but also exhibited some of the dominant characteristics of the PDO time-series (Figure 6).

Recruitment followed the change in the mean of the PDO, declining from the 1920s to the early 1940s, then increasing and remaining high until the late 1970s, then again declining. That variability was greater with increased fishing. It is difficult to pick out an increase in variability on 4–6-year time-scales in the generic salmon series, but one can see the increase in variability on that time-scale from the generic cod fished to FLEP = 0.3 from 1930 to ~1960, consistent with the bout of variability indicated in the PDO spectrum (Figure 6).

In the wavelet spectrum of that recruitment series (Figure 8), variability was generally greater at longer periods and increased in magnitude with fishing, as in the white noise case (Figure 5). In the spectral response of the generic long-lived cod, the three decades of variability on time-scales of 4–8 years in the PDO (1930–1960; i.e. the white contours) produced minimal variability in recruitment in the absence of fishing, then increasing variance as fishing increased (Figure 8a–c), becoming strongest when the mean age of spawning was 6 years. For the short-lived salmon, where the cohort resonance is inherently stronger, the years 1930–1960 produced strong variability at a period of 4–8 years, even in the absence of fishing (Figure 8d), and it became stronger with fishing (Figure 8e and f).
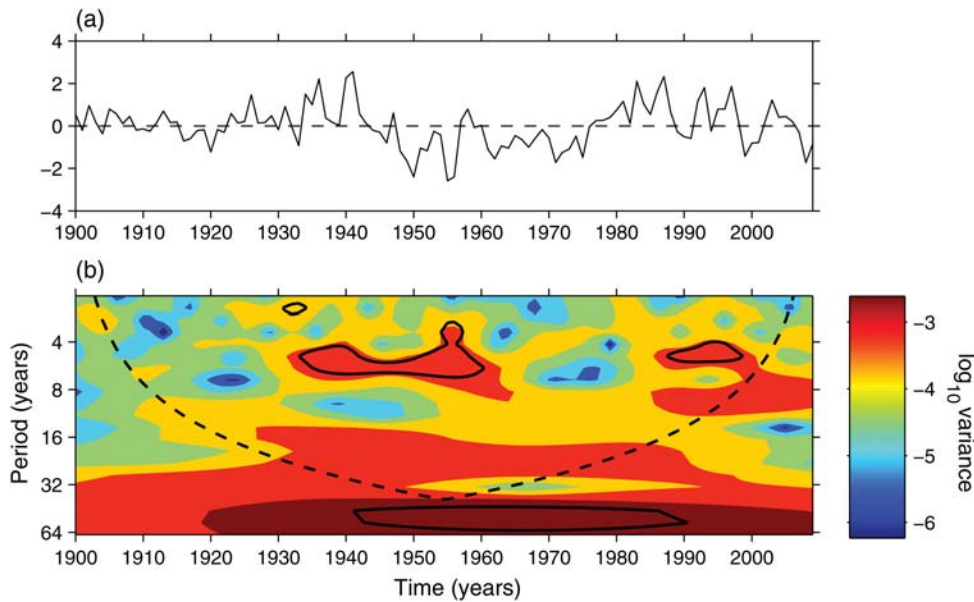
Figure 6. The time-series (a) and wavelet spectrum (b) of the PDO for the 20th century (Mantua *et al.*, 1997; http://jisao.washington.edu/pdo/). Lines and units as in Figure 1.
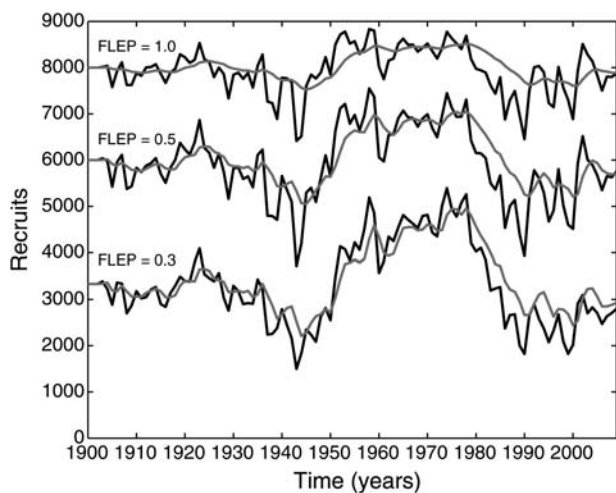
Figure 7. Recruitment time-series for the generic cod species (grey lines) and the generic salmon species (black lines) from simulations with fluctuations in survival driven by the PDO time-series from the 20th century, with a CV of 0.344. The three series for each generic species are unfished (top plot), fished to FLEP = 0.5 (middle plot), and fished to FLEP = 0.3 (bottom plot).

Comparison of age-structured models to ecosystem model approximations

The time-series resulting from possible departures from the real age-structured populations illustrated potential errors in prediction as fishing increased from $F = 0$ to a value that produced a collapsing population (FLEP = 0.2) at $t = 100$ years for the nominal cases (i.e. the cases with $a = 4$ in Figure 9a, slope equal to α in b, and true age structure in c). In the first example, underestimating the age of maturity and first fishing resulted in a greater estimate of the initial recruitment level, but a more rapid decline in the equilibrium value of recruitment (Figure 9a). In that case, populations

would be predicted to collapse earlier than they actually would collapse. That case also was less variable than the cases with the true value and the overestimate. The spectrum of the true age-structured model (Figure 10d) displayed intensification of cohort resonance as fishing increased over time and the mean age declined. The case with *a* overestimated had a spectrum similar to that of the true value, regardless of the misspecification of the age of maturity and first fishing (i.e. the black contours in Figure 10e followed the "correct" white contours relatively well). The spectrum with the underestimate (Figure 10b) displayed less variance in the range of cohort resonance (near 4 years) than the properly parametrized model.

In the second example, overestimating the slope of the egg–recruit relationship at the origin resulted in populations appearing to persist much longer than they actually would persist, and *vice versa* for an underestimate of that slope (Figure 9b). The overestimate had the same amount of variability as the true value, but the time-series for the underestimate had less. The spectrum for the example with an overestimate of the slope (Figure 10f) closely matched that of the true age structure, whereas that from the underestimate did not (Figure 10b).

The third and the fourth cases involved structural assumptions regarding the population model. When the true age structure was approximated by a population model with lumped mature ages, the population was predicted to continue to persist long after it would actually collapse (Figure 9c). The spectrum of this example (Figure 10c), however, was similar to the spectrum for the true age-structured model (Figure 10d), with greater variability at short periods. In the fourth case, when the true age structure was approximated by a stage-structured model, the decline was slower than the true age-structured model, indicating the population being predicted to collapse later than the actual time (Figure 9c). This approximation exhibited far less variability than the true age-structured model. The stage-structured model (Figure 10g) produced much less relative variability at periods <4 years than the age-structured model (Figure 10d).
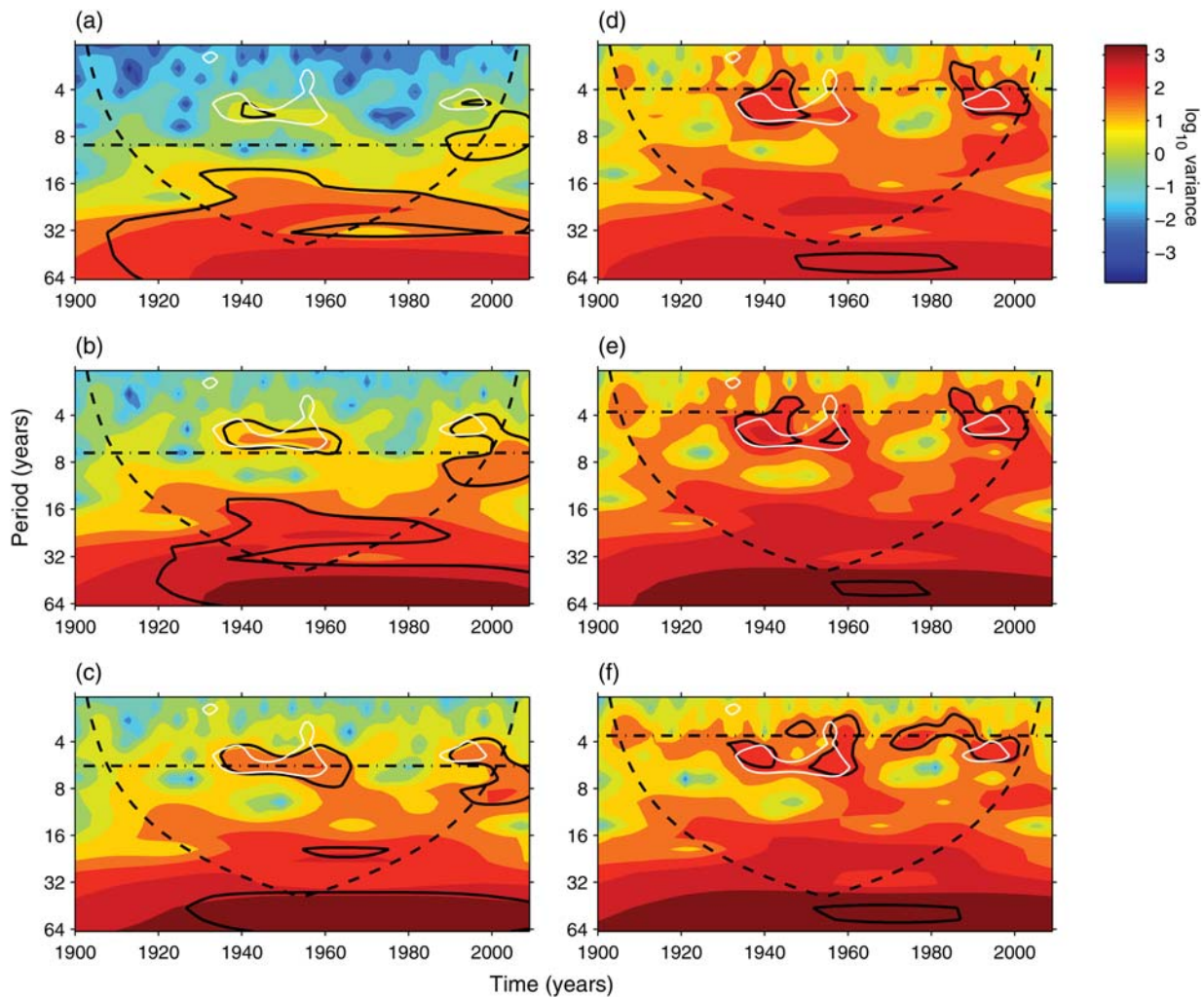
Figure 8. Wavelet spectra for the recruitment of the generic cod species (a–c) and generic salmon (d–f) time-series forced by PDO (Figure 7). The three levels of fishing are unfished (a and d), fished to FLEP = 0.5 (b and e), and fished to FLEP = 0.3 (c and f). White contours indicate significance regions for the forcing spectrum in Figure 6. Other lines and units as in Figures 1 and 5.

Discussion

The responses of age-structured populations to stochastic environmental forcing demonstrated here will likely be a dominant component of the behaviour of UTL species under the combination of fishing and climate change. As fishing increases, the overall population variability increases (Figures 3–5 and 7–10; Table 1), until a point is reached where the declining equilibrium causes the overall variability to decline. These changes in variability are accompanied by an increasing sensitivity of populations to specific frequencies of fluctuations in the ocean environment. One time-scale is the dominant age of spawning, the generational time-scale, which is set by the species' life history. The second time-scale involves gradual change at low frequencies, which is independent of the species' life history. A future ocean affected by changing climate will likely include important variability at both frequencies.

This population behaviour has practical consequences for both future fisheries management and our understanding of the biophysical interactions that underlie future change in UTLs. Regarding the former, population sustainability depends on abundance and the level of variability. Knowing how these could change

and why they could change differently for different species will aid in anticipation of management needed and the stocks likely to be in jeopardy. Regarding the latter, current approaches towards understanding different responses of marine populations at different locations currently focus on spatial and temporal variability in only the physical conditions. Our results outline the specific contributions of population dynamics to differences in population responses to physical conditions.

Our examination of the performance of models that do not have the correct form, either because of incorrect parameter values or incorrect model structure, yields guidance for current predictive modelling of future dynamics of UTLs. Equilibrium behaviour was sensitive to underestimates of the age of maturity, but data on the age of maturity are frequently readily available or can be easily obtained. It is not surprising that the rate of population decline is sensitive to the specification of the slope of the egg–recruit relationship, because that parameter is fully understood to be a critical one for fisheries persistence (Sissenwine and Shepherd, 1987; Myers *et al.*, 1999). This result underscores the importance of using accurate estimates, possibly available from

fisheries data, of this parameter, and cautions against leaving its value to arise as an emergent property of trophic interactions in an ecosystem model (Christensen and Walters, 2004).

Choosing an adequate model structure depends on an understanding of the mechanism underlying much of the variability in age-structured populations, namely cohort resonance. This mechanism depends on the echo effect (Sykes, 1969), the concept that a birth pulse at one time would affect the number of births later when that cohort began to reproduce, with a lag equal to the dominant age of spawning. This means that environmental variability with a period equal to the age of dominant spawning will be selectively amplified. Accurately depicting the age-dependence of reproduction is vital to accurate depiction of the lags in the response to a variable environment. That is the basic reason why the model with lumped adults resulted in a spectral sensitivity quite close to the actual age structure. The lumped model did not accurately depict the rate of decline, but that problem likely arose because the lumping produced a slower decline in FLEP with *F*, an artefact that could be reduced by terminating the age structure at the same maximum age as that of the actual population. The stage-structured model, conversely, smoothes the age structure, because individuals begin passing out of each 2-year stage the year after they move into it. This disrupts the echo effect that would be present in a real population and produces dramatically different spectral response to environmental variability (Figure 10g).

The current direction in predictive modelling of the effects of climate change on ocean ecosystems appears to be moving towards descriptions based on foodwebs within ecosystem models. The results presented here indicate substantial opportunities for these approaches to err in their predictions for age-structured populations, if the models parametrize population processes incorrectly or if they adopt a model structure that does not faithfully reproduce important characteristics of age-structured populations, i.e. changes in equilibria and cohort resonance variability. Because the questions asked in ecosystem modelling ultimately involve the relative abundances of various species, if they do not include adequate depiction of age structure, the answers obtained will be subject to errors. Detailed commentary on the specific strengths and weaknesses of the many ecosystem modelling approaches currently in use is beyond the scope of this paper, but that topic has been addressed by several comprehensive reviews, some of which also advise against ignoring population data and population approaches (Hollowed *et al.*, 2000; Plagányi and Butterworth, 2004; Plagányi, 2007; Fulton, 2010; Rose *et al.*, 2010).

In some circles, population models have become disfavoured based on a belief that overharvesting and low population abundances in fisheries are the result of a "single-species" approach (Rose *et al.*, 2010). This tendency to imply that single-species population dynamics approaches are the root cause of fishery failures might be misplaced (Hilborn, 2007). Fisheries fail for many reasons, but most would agree that uncertainty plays a large role
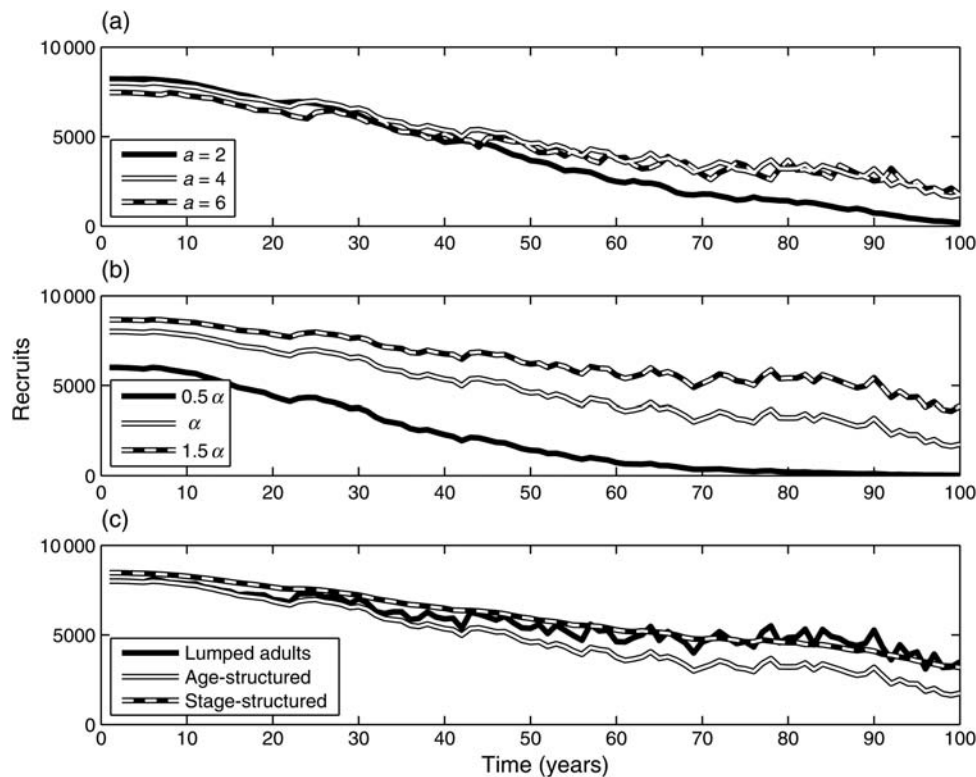
Figure 9. Examples of the consequences of various departures from an accurate representation of the age-structured dynamics of the generic cod species. The simulations are driven by independent white noise series causing a CV of 0.354 in the survival rate s_1. The fishing increases linearly from no fishing to values causing a decline in FLEP from 1.00 at $t = 0$ to 0.2 at $t = 100$. The departures include: (a) errors in the specification of the age of maturity for the generic cod model, (b) errors in the specification of the slope of the Beverton–Holt egg–recruit function at the origin, and (c) the use of two different approximations to age-structured models, a lumped model with a plus group, and a stage-structured model.
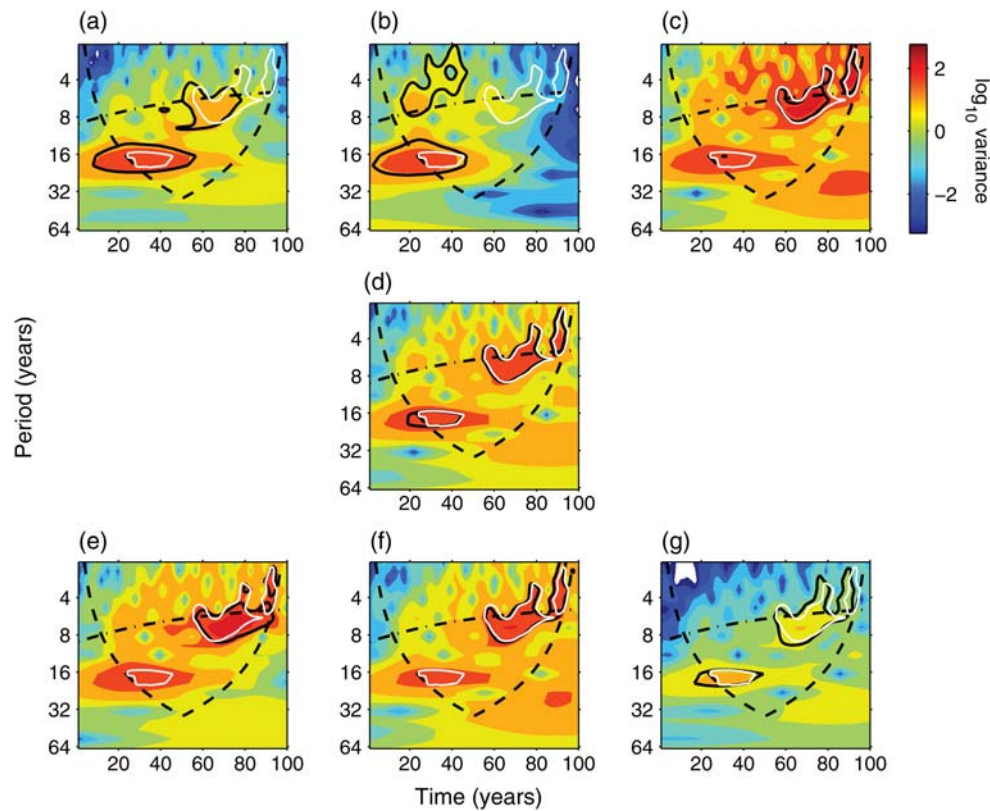
Figure 10. Wavelet spectra for the recruitment of the generic cod species for the time-series in Figure 9, with (d) the fully age-structured iteroparous model with mean age of reproduction $a = 4$ years and stock–recruit slope α; the same model with (a) $a = 2$ years, (e) $a = 6$ years, (b) slope $= 0.5\ \alpha$, (f) slope $= 1.5\ \alpha$; (c) lumped-adult age-structure model; and (g) stage-structured model. Each time-series was detrended by translating it about a low-pass filtered version of itself [MATLAB function "filtfilt" with a rectangular window of length 10 (Mathworks Inc., 2009)]. White contours indicate the significance levels for the fully age-structured iteroparous model (d); the white contours have been jittered slightly forward in time to make both sets of contours visible. The dash–dot line in each panel is plotted at the mean age of spawning for the iteroparous model at the equilibrium determined by the level of fishing mortality at that point in time. Other lines and units as in Figure 1.

(Ludwig *et al.*, 1993; Botsford *et al.*, 1997) and that a substantial component of that uncertainty is in the answer to the question, "How much can we fish before this population collapses?" Single-population fisheries management has identified the nature of the egg–recruitment relationship at low abundance as a significant determinant of the answer to that question (Sissenwine and Shepherd, 1987; Mace and Sissenwine, 1993; Myers *et al.*, 1999). Ignoring this basic uncertainty in favour of models that essentially estimate the egg–recruitment relationship based on their choice of parameters in equally uncertain feeding relationships (Plagányi and Butterworth, 2004) apparently is not a viable means of improving prediction of UTLs under future climate change.

The age-structured model used here to illustrate the effects of declining equilibria and cohort resonance is not necessarily intended to be a sufficient model for projection of future abundance or to replace ecosystem models. One shortcoming is that it has no ecosystem effects. For example, the long-term changes in survival simulated here could be because of changes in predator or prey abundance, such as the changes in zooplankton prey apparently driving the fluctuations in marine survival of coho salmon in the California Current (Peterson and Schwing, 2003). On the other hand, Murdoch *et al.* (2002) have suggested that even when UTLs are linked to complex foodwebs, single-species

models could afford a realistic representation of their behaviour when those populations are generalist consumers. Conversely, Travers *et al.* (2007) recommend greater representation of two-way interactions between functional groups in ecosystem models. A second omission from our age-structured model is that for simplicity we did not allow individual growth rates to vary in response to environmental forcing. Adding this effect would have produced similar results, but likely with greater magnitude of the cohort resonance mode of variability (see Worden, *et al.*, 2010, for further details).

It seems incongruous that even as models designed to predict responses to future climate change abandon knowledge developed from the study of population dynamics, population mechanisms are widely invoked to explain current ecological responses to climate and fishing. For example, Planque *et al.* (2010) summarize the combined effects of fishing and climate change on marine systems and the mechanisms that produce those effects, including mention of the cohort resonance phenomenon described by Bjørnstad *et al.* (2004), but not the effects of fishing on it. In a similar review, Perry *et al.* (2010) describe the effect of fishing on the sensitivity of populations to climate change for two demographic mechanisms: (i) the reduction in buffering capacity by the reduction in older ages in a population, and (ii) a change in

spawning dynamics because of this same truncation. Buffering capacity refers to an ability of populations with many age classes to continue to persist through longer periods of adverse recruitment conditions than can occur in populations with few age classes (Murphy, 1968). We addressed this topic directly, because we focused on relationships between time-scales of variability in the environment and the age structure of the population (e.g. Figure 2a and b).

The representation of age-structured populations of UTLs in models could be substantially improved with modest additional effort. For example, the rate of the decline of equilibrium with fishing in the lumped model could be increased to a realistic value by removing fish beyond the maximum age as noted above. Adjusting the egg–recruit relationship to be as close as possible to existing observed data could make the lumped model a good representation of actual age structure. Models with lumped mature ages might represent the dynamics of the true age structure well, but stage-structured models and size-structured models with similar numerical solutions (i.e. moving specific fractions from size class to size class; Hall *et al.*, 2006) will not.

The steps that could be taken to resolve the problems in predictions of age-structured UTLs described here do not fall outside the general scheme developers of ecosystem models envision as the use of their models. Mostly, the scheme involves not just a single ecosystem model, but an ensemble of models that approach prediction from different points of view (Fulton 2010). More specifically, some do not envision ecosystem models as replacing single-species models, at least for current day assessments. For example, Christensen and Walters (2004) say "many of the questions ... have their root in an assumption that EwE is somehow intended to supplant or replace single-species assessment methods. This is clearly not the case." In the same publication, they describe ways to change the value of steepness of the stock–recruitment relationship directly, rather than letting it arise as an emergent property. In addition, developers of ecosystem models emphasize that use of such tools should focus on strategic evaluation of changes in ecosystem components compared across alternative scenarios (e.g. of management or climate) rather than on tactical assessment and accurate prediction (Fulton, 2010; Rose *et al.*, 2010).

In summary, ignoring the true age structure and stock–recruitment relationships of UTL species results in serious difficulties in forecasting accurately the response of those species to future climate changes. However, these problems can be avoided, if care is taken to represent accurately the population age structure and to ensure that the models are consistent with existing population data.

Acknowledgements

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